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A GASTROPOD *PATELLA ULYSSIPONENSIS* GMELIN, 1791 (GASTROPODA: PATELLIDAE) FROM THE CAUCASIAN BLACK SEA SHELF: BIOLOGICAL INVASION OR RECOVERY OF THE NATIVE POPULATION?

© 2025 **Zh. Selifonova[1], M. Reneva[2], O. Poltarukha[3], and A. Boran-Keshishyan[1]**

[1]Admiral Ushakov Maritime State University, Novorossiysk, Russian Federation
[2]Sochi National Park, Sochi, Russian Federation
[3]Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, Russian Federation
E-mail: *selifa@mail.ru*

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In spring 2023, an abundant population of adult gastropods *Patella ulyssiponensis* Gmelin, 1791 was recorded in the Sochi port area. *P. ulyssiponensis*, also known as a limpet, is an inhabitant of contour biotopes and a crawling edible gastropod. This species is listed in Red Data Books of the Black Sea, the Crimea, and Sevastopol and still does not occur on shelves of the Crimea, Ukraine, Romania, Bulgaria, and Turkey. It was not registered on the Caucasian shelf since the middle of the XX century. The paper provides data on distribution, morphological structure, and settlement density of *P. ulyssiponensis* sampled in the Sochi port area in June 2023. According to the severity of radial ribs and their association into bundles, the position of the crown, the morphometry of the shell itself, the color of the shell inner surface, and the integrity or serration of the peristome, the found species was assigned to *P. ulyssiponensis*. In the Black Sea, the limpet is known as *Patella tarentina* Salis Marschlins, 1793, *P. caerulea* var. *tenuistriata* Weinkauff, 1880, and *P. pontica* Milaschewitsch, 1914 (syn.). In earlier works on the Black Sea, it was combined with *P. caerulea* Linnaeus, 1758 endemic to the Mediterranean Sea. *P. ulyssiponensis* abundance reached 240–320 ind.·m^{-2} and was higher at the station on the outer side of the southern pier than in the beach area. The limpets we registered were somewhat smaller than those previously noted for the Black Sea. The maximum length of the shell for molluscs of the Sochi port area reached 43.0 mm; width, 17.3 mm; and height, 20 mm. However, these individuals had a higher shell than those of the Black Sea population and the population from the northern Aegean Sea; this is typical for inhabitants of the water's edge. The ratios of the shell height to its length were (0.43 ± 0.05) and (0.45 ± 0.07) for the first and second study areas, respectively. *P. ulyssiponensis* reinvasion to the northeastern Caucasian shelf could be governed by anthropogenic transfer by ships and by natural dispersal. Along with other aspects revealed in recent years in the Black Sea ecosystem, this finding illustrates positive changes in gastropod fauna from the Caucasian shelf.

Keywords: *Patella ulyssiponensis*, distribution, morphometry, density, Sochi port

Since the late 1990s, rare species of zooplankton and zoobenthos more and more often occur in various areas of the Black Sea: the ones that had disappeared during severe pollution, eutrophication of the basin, and pressure by an invasive predator – the warty comb jelly *Mnemiopsis leidyi* A. Agassiz, 1865. The tendency toward ecosystem recovery on the Crimean and Caucasian shelves during

the early XXI century coincided with a similar trend observed along the northwestern coast of Ukraine, Romania, and Bulgaria, as well as on the Black Sea coast of Turkey [Arashkevich et al., 2015; Aydın et al., 2021; Filimon, 2020; Kucheruk et al., 2002; Revkov, Boltacheva, 2022; Revkov et al., 2019; Selifonova, 2012; Todorova et al., 2022; *etc.*]. This phenomenon is associated with a shift of the Black Sea ecosystem from a eutrophication phase to a de-eutrophication phase and with a gradual recovery of pelagic and benthic communities [Oguz et al., 2008; Yunev et al., 2007; Zaika, 2011]. Since the 2000s, an increase in abundance of certain populations of previously rare, endangered native species is recorded, and it is accompanied by a mass introduction of invasive, alien species brought in *via* ballast water of merchant ships [Alexandrov, 2004; Çinar et al., 2021; Seebens et al., 2019; Selifonova, 2018; Selifonova et al., 2021; Shiganova et al., 2012; *etc.*].

One of the Black Sea species that disappeared or experienced a drastic population decline during the ecological crisis of the ecosystem is a gastropod *Patella ulyssiponensis* Gmelin, 1791, also known as a limpet. Its absence in published data and in a mollusc collection of the Sochi Geographical Society assembled in the 1960s seems to evidence for the fact that *P. ulyssiponensis* vanished from the Caucasian shelf of the Black Sea in the middle of the XX century. This species was considered critically endangered and was listed in Red Data Books of the Black Sea, the Crimea, and Sevastopol [Black Sea Red Data Book, 1999; Revkov, 2011, 2015]. According to data available, this mollusc still does not occur on shelves of Ukraine, Romania, Bulgaria, and Turkey. The last time *P. ulyssiponensis* was recorded in the Crimea in 2007; however, it is not listed in the Red Data Book of Krasnodar Territory [2017]. Since 2012–2014, researchers from the Sochi Geographical Society, L. Sonicheva and I. Antonova, periodically found single *Patella* spp. along the coast from Lazarevskoye to Adler [Reneva, 2024]. In 2019–2020, the authors observed the mollusc developing in significant numbers not only in Sochi vicinity, but also in Abkhazia, along Pitsunda and Gudauta coasts. In 2017, the online report documented *Patella* spp. finding off the Georgian coast, south of Batumi [Kurakin, 2023]. Observed molluscs were initially identified by the author as *Patella tarentina* Salis Marschlins, 1793, but this name is a junior synonym for *P. ulyssiponensis*. Notably, another Mediterranean species, *Patella caerulea* Linnaeus, 1758, has been registered at various sites of the Black Sea coast of Turkey [Aydın et al., 2021; Çulha et al., 2007; Güngör, Turan, 2019]. In April 2023, we noted an abundant population of molluscs tentatively identified as *P. ulyssiponensis* in the Sochi port area. It raises a critical question: is it a biological invasion of a Mediterranean species, or is it the recovery of the previously extinct native population of *P. ulyssiponensis* on the Caucasian shelf?

In this study, we clarify the taxonomic identity and discuss the distribution of a gastropod *Patella ulyssiponensis* registered in the Sochi port area. We provide data on the morphological structure and population density of this species as well.

MATERIAL AND METHODS

For laboratory analysis, *P. ulyssiponensis* specimens were sampled on 22 and 26 June, 2023, in the pseudolittoral zone on buoys and breakwaters along the outer side of the southern pier of the Sochi port (station 1) and on a breakwater near the beach of the “Alexandriisky Mayak” apartment complex (station 2). A schematic map of the sampling area is shown in Fig. 1. Molluscs were sampled manually at depths of less than 1 m with a pocketknife and a 25 × 25 cm frame (in triplicate); 144 ind. in total. Live specimens were measured, weighed, and fixed in 70% ethanol. Gastropods were identified

down to the species level based on morphological analysis following the papers [Christiaens, 1973; Golikov, Starobogatov, 1972]. Taxa are listed in accordance with the current edition of the WoRMS Editorial Board [2023].

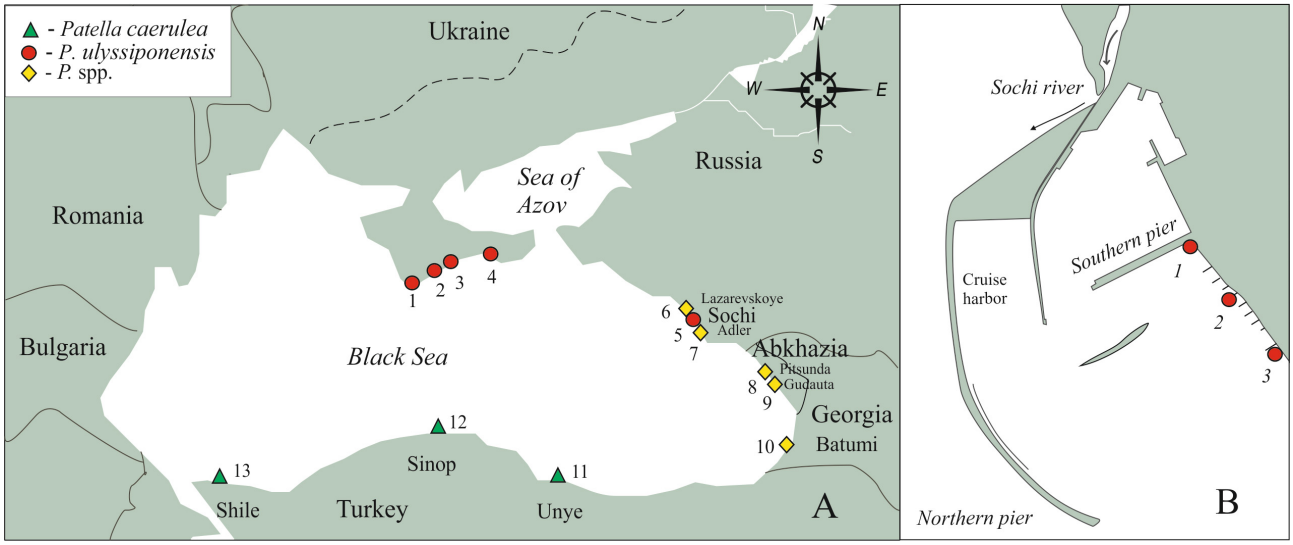

Fig. 1. A, schematic map of records of gastropods of the genus *Patella* in the Black Sea. *Patella ulyssiponensis* (●): 1–4, [Revkov, 2015]; 5, Selifonova *et al.* (our data). *Patella* spp. (♦): 6, 7, Sonicheva L. (Sochi Geographical Society, oral report); 8, 9, Antonova I. (Sochi Geographical Society, oral report); 10, [Kurakin, 2023]. *Patella caerulea* (▲): 11, [Aydın et al., 2021]; 12 — [Çulha et al., 2007]; 13 — [Güngör, Turan, 2019]. B, stations of the mollusc records (1–3) and sampling: 1, outer side of the southern pier of the Sochi port; 2, breakwater near the beach of the "Alexandriisky Mayak" apartment complex

RESULTS

Taxonomic, morphological, and ecological characteristics of molluscs.

Class Gastropoda Cuvier, 1795

Subclass Patellogastropoda Lindberg, 1986

Subfamily Patelloidea Rafinesque, 1815

Family Patellidae Rafinesque, 1815

Genus *Patella* Linnaeus, 1758

Patella ulyssiponensis Gmelin, 1791 (Figs 2, 3).

Material. Sta. 1, 80 ind., shell length of 21.4–43.0 mm. The Black Sea, a buoy, outer side of the southern pier of the Sochi port (N43.578912°, E39.717003°), smooth concrete surface. Fouling: algae of the genera *Ulva*, *Cladophora* (Chlorophyta), *Ceramium*, *Polysiphonia* (Rhodophyta), and *Cystoseira* (Phaeophyta); hydroids (Hydrozoa); sedentary forms of polychaetes of the genus *Spirorbis* (Polychaeta); a bay barnacle *Amphibalanus improvisus* (Darwin, 1854) (Cirripedia); bryozoans (Bryozoa); and bivalves *Mytilus galloprovincialis* Lamarck, 1819 and *Magallana gigas* (Thunberg, 1793) (Bivalvia). At the site of cracks and hollows of the substratum, there were aggregations of small mussels (less than 20–30 mm in length). Samplers: M. Reneva and A. Boran-Keshishyan (22.06.2023).

Sta. 2, 64 ind., shell length of 19.1–35.1 mm. The Black Sea, a breakwater near the beach of the "Alexandriisky Mayak" apartment complex (N43.575430°, E39.723044°), smooth concrete surface. Fouling: algae *U. rigida* (Chlorophyta), *Cystoseira* (Phaeophyta), and a coralline alga

Phymatolithon calcareum (Pallas) W. H. Adey & D. L. McKibbin ex Woelkering & L. M. Irvine, 1986 (Rhodophyta); hydroids (Hydrozoa); sedentary polychaete worms of the genus *Spirorbis* (Polychaeta); a bay barnacle *A. improvisus* (Cirripedia); bryozoans (Bryozoa); a mussel *M. galloprovincialis* (Bivalvia); and a hermit crab *Clibanarius erythropus* (Latreille, 1818) (Decapoda). Samplers: M. Reneva and A. Boran-Keshishyan (26.06.2023).

Fig. 2. Settlement of a gastropod *Patella ulyssiponensis* on the buoys of the Sochi port

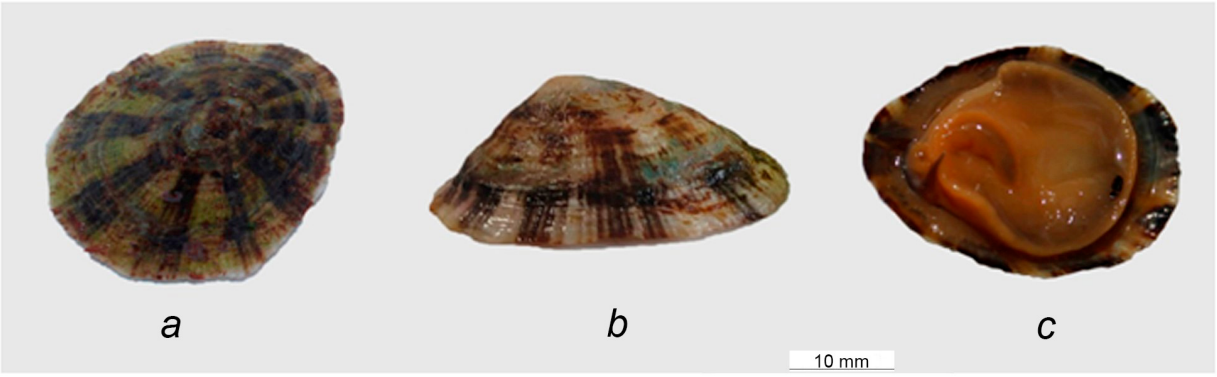

Fig. 3. *Patella ulyssiponensis*: view from above (a); side view (b); view from below (c)

The sampled molluscs are deposited in collections of the Admiral Ushakov Maritime State University (laboratory of marine biology and ecology), the A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS (department of benthic ecology), and the Sochi Geographical Society.

P. ulyssiponensis head and cephalic tentacles are semi-transparent and white, with a yellow buccal disc. The foot is pear-shaped or oval; it is orange, though paler in smaller individuals. The mantle margin is semi-transparent, typically darker than the body, and yellowish-white.

Alternating long and short tentacles of white or yellowish coloration line the mantle margin. In live molluscs, the mantle margin may slightly protrude beyond the shell. In *Patella* individuals studied, the anterior end of the shell was often narrower than the posterior one. The shell apex was centrally positioned or slightly shifted forward.

Externally, the shell exhibits faint ribbing, with an irregular, often serrated edge. Internally, the shell is milky white, occasionally with a bluish tint, and features prominent yellow-orange blotches.

For species identification, we referenced the classic taxonomic revision of the genus *Patella* [Christiaens, 1973]. Diagnostic traits outlined in this paper agree well with subsequent studies. Thus, for specimens from Algerian coastal waters [Beldi et al., 2012], key differences between *P. caerulea* and *P. ulyssiponensis* were rooted in shell morphology, foot coloration, and radula length. *P. caerulea* has a thinner, more rounded shell, with a slightly eccentric apex and a nacreous bluish-gray interior. *P. ulyssiponensis* features a thicker, elongated shell, with a centrally positioned apex and a porcelain-white interior with faint bluish tint. *P. caerulea* exhibits a gray foot sole, while *P. ulyssiponensis* has a yellow-orange one. *P. caerulea* has a radula approximately 1.5 times the shell length, whereas *P. ulyssiponensis* has a shorter radula, roughly equal to the shell in its length [Beldi et al., 2012]. However, other researchers [Christiaens, 1973; Fischer-Piette, 1935; Öztürk, Ergen, 1999] report that differences in radula length between the two species are minimal. This feature is too variable to serve as a reliable diagnostic trait.

These findings agree well with results of *Patella* studies in coastal waters of the Tyrrhenian Sea [Cretella et al., 1994] emphasizing the morphology of soft body parts. According to this paper, *P. caerulea* has a gray head with dark-gray cephalic tentacles and a cream-colored buccal disc. The foot sole is dark-gray along its edge, occasionally with a bluish tint, while the central area is cream-colored. Along the body sides, *P. caerulea* exhibits a mix of long, medium, and short tentacles, with groups of 5–8 alternating medium and short tentacles positioned between 2 long ones. In contrast, *P. ulyssiponensis* features a white head, whitish cephalic tentacles, and a yellow buccal disc. The foot sole is uniformly apricot, yellow, or cream-colored. Along the body sides, there are alternating long and short tentacles only. The results of a comparative analysis of proteins *via* gel electrophoresis carried out in this study and in an earlier paper [Sella et al., 1989] confirm that *P. caerulea* and *P. ulyssiponensis* are closely related species, but separate ones.

The examined individuals were identified as *P. ulyssiponensis* based on the prominence of radial ribs and their grouping into bundles, the position of the shell apex, shell morphometrics, internal shell coloration, integrity or serration of the peristome, soft tissue pigmentation, and the structure of lateral tentacles. Major distinctions between *P. ulyssiponensis* and *P. caerulea* lie in shell morphology and foot sole coloration. As noted above, *P. caerulea* has a thinner and more rounded shell, with a slightly eccentric apex and a nacreous bluish-gray interior. *P. ulyssiponensis*, in contrast, features a thicker and elongated shell, with a centrally positioned apex and a porcelain-white interior, with faint bluish tint. *P. caerulea* has a gray foot sole, while *P. ulyssiponensis* has a yellow-orange one [Beldi et al., 2012]. As for other *Patella* species, *Patella rustica* Linnaeus, 1758 is distinguished by its dark internal shell coloration and brown foot sole, contrasting with the species studied [Beldi et al., 2012]. *Patella vulgata* Linnaeus, 1758 shares the yellow foot sole coloration with *P. ulyssiponensis* (however, it can be gray as well), but differs in gray exterior and yellow-orange interior shell pigmentation [Beldi et al., 2012]. *Patella ferruginea* Gmelin, 1791 also resembles *P. ulyssiponensis* in its yellow-orange foot sole

but typically features a gray marginal band. Moreover, *P. ferruginea* possesses long, medium, and short tentacles along the mantle margin. Long tentacles align with radial ribs, while groups of 9–13 alternating medium and short tentacles occupy the space between them [Cretella et al., 1994]. Importantly, *P. ulyssiponensis* exhibits only alternating long and short tentacles. *Patella depressa* Pennant, 1777 differs from the species studied in its gray-black foot sole and orange or brown internal shell coloration [Beldi et al., 2012].

Morphometric population structure. Shell of *P. ulyssiponensis* of the Sochi port area is cap-shaped, relatively thick, and oval (rarely rounded); it has a pointed apex and distinct growth rings. Based on these rings, we can conclude that the age of the molluscs ranged 1 to 5 years. Shell dimensions varied as follows: length, 19.1–43.0 mm; width, 15.2–43.0 mm, and height, 7.0–20.0 mm. Ratios of shell height to its length were (0.43 ± 0.05) and (0.45 ± 0.07) for the first and second habitats investigated, respectively. On average, *P. ulyssiponensis* of the Sochi port area were slightly larger. Detailed morphometric data on the specimens analyzed are provided in Table 1.

Table 1. Morphometric structure of *Patella ulyssiponensis* population (n = 144) in the Sochi port area

Parameter	Station 1, outer side of the southern pier of the Sochi port	Station 2, breakwater near the beach of the "Alexandriisky Mayak" apartment complex
Length, mm*	34.4 ± 1.1	26.9 ± 0.5
Min	21.4	19.1
Max	43.0	35.1
Width, mm*	27.9 ± 1.2	21.7 ± 0.5
Min	15.2	17.3
Max	43.0	29.1
Height, mm*	14.5 ± 0.6	12.2 ± 0.3
Min	7.0	8.1
Max	18.1	20.0
Height/length*	0.43 ± 0.05	0.45 ± 0.07
Min	0.33	0.35
Max	0.53	0.62
Weight, m*	5.99 ± 0.5	3.68 ± 0.28
Min	0.9	1.1
Max	10.06	6.67

Note: *, mean ± standard deviation is indicated.

Species population density and weight characteristics. *P. ulyssiponensis* population density ranged within 240–320 ind.·m^{-2}, mean of (260 ± 75.7) ind.·m^{-2}. Weight varied 3.68 to 5.99 g·m^{-2}, mean of (4.8 ± 0.3) g·m^{-2}. Density was higher at sta. 1, on the outer side of the southern pier of the Sochi port.

DISCUSSION

Should *P. ulyssiponensis* be considered a Mediterranean biological invader, or do we deal with the recovery of the native Black Sea population? To clarify this issue, we need to analyze the taxonomic status of limpets from the Black and Mediterranean seas. Available literature provides divergent views on the origin of this species. Below, we review up-to-date information supplemented by literature data on *P. ulyssiponensis* biology.

A mollusc *Patella ulyssiponensis* (*P. tarentina* Salis Marschlins, 1793; *P. caerulea* var. *tenuistriata* Weinkauff, 1880 [Ostroumov, 1983]; *P. pontica* Milaschewitsch, 1914; *P. caerulea pontica* Milaschewitsch, 1916 [Il'ina, 1966]) belongs to the class Gastropoda and the family Patellidae (sea limpets) [Golikov, Starobogatov, 1972; Kantor, Sysoev, 2006; Milaschewitsch, 1916; WoRMS, 2023] (see Fig. 3).

In agreement with the classical synopsis of the Black Sea and Sea of Azov fauna [Golikov, Starobogatov, 1972], two *Patella* species inhabited the Black Sea: *P. ferruginea* and *P. tarentina*. The latter one, according to the authors of the synopsis, is closely related to *P. caerulea* and penetrated both the Black Sea and Sea of Azov. Notably, the researchers assert that *P. caerulea* was absent from the Black Sea, even from the Bosphorus area, while both *P. tarentina* and *P. caerulea* inhabit the Mediterranean Sea and the Atlantic coast of Europe as far north as England. They also clarify that *P. ferruginea* had not been recorded in the Black Sea for the last 50 years. Importantly, the genus *Patella* is not mentioned in the monograph on the Sea of Azov molluscs [Anistratenko et al., 2011].

Biodiversity of the Black Sea *Patella* representatives is interpreted quite differently in a later monograph on the Black Sea gastropods [Chukhchin, 1984]. According to this author, only one species (a highly variable one), *P. caerulea*, inhabited the Black Sea; it is considered as an endemic to the Mediterranean Sea.

In contrast, the catalogue of Gastropoda of Russia and adjacent countries [Kantor, Sysoev, 2006] lists three *Patella* species for the Black Sea: *P. caerulea*, *P. ferruginea*, and *P. ulyssiponensis*. There, the latter species is treated as a synonym for *P. tarentina* and is reported for the Sea of Azov as well. As additionally noted, *P. ferruginea* may have become extinct in the Black Sea.

P. ulyssiponensis occurrence in the Black Sea is reported not only by domestic researchers, but also by foreign ones [Katsanevakis et al., 2008]. A recent paper [Gomes et al., 2021] based on genetic and biogeographic studies proves that *P. aspera* Röding, 1798 is a synonym for *P. ulyssiponensis*, although the World Register of Marine Species currently recognizes them as separate species. According to WoRMS [2023], *P. tarentina*, *P. caerulea* var. *tenuistriata*, and *P. pontica* are synonyms for *P. ulyssiponensis*. The latter species, along with *P. caerulea* and *P. ferruginea*, is now considered as a separate and valid one. However, as mentioned above, *P. ulyssiponensis* was often conflated with a highly variable species *P. caerulea*, a Mediterranean endemic [Chukhchin, 1984]. Thus, the assumption about the independent status of *P. ulyssiponensis* and its occurrence in the Black Sea can now be considered as well-supported and proved.

Morphometric analysis of shell structure is crucial for mollusc taxonomy. The specimens we examined were generally smaller, but had higher shells compared to those from the Black Sea population and a population of the northern Aegean Sea (the Gulf of Saros), where *P. ulyssiponensis* had an average shell length of 36.4 mm (maximum of 48.6 mm), width of 28.9 mm, and height of 9.5 mm [Öztürk, Ergen, 1999]. According to [Golikov, Starobogatov, 1972], the Black Sea specimens can reach the length of 45.0 mm, width of 30.0 mm, and height of 14.0 mm. Flatter shells of Mediterranean *Patella* representatives compared to the Black Sea molluscs are known for a long time and are typical of limpets inhabiting the intertidal zone [Chukhchin, 1984]. Thus, the Black Sea *P. ulyssiponensis* have some morphological distinctions from the Mediterranean Sea ones. This raises the question of whether the differences reflect intraspecific variability, or it is reasonable to consider the Black Sea populations of *P. ulyssiponensis* as a separate subspecies or even species.

We found no published data on *P. ulyssiponensis* reproduction and development. However, based on what is known about *P. caerulea* [Aydın et al., 2021; Chukhchin, 1984; Ferranti et al., 2018; Wanninger et al., 1999a, b], it is plausible to infer that *P. ulyssiponensis* is also a perennial polycyclic species with protandric hermaphroditism and a short planktonic larval stage. Its reproduction likely occurs in autumn (in October and November), the same as in *P. caerulea*.

Like other representatives of the genus, *P. ulyssiponensis* feeds by scraping bacterial–algal films from rocks. Also, literature data [Ayas, 2010; Silva et al., 2008] evidence for the fact that this mollusc feeds on multicellular green algae, *Ulva lactuca* Linnaeus, 1753 in particular. However, its primary diet is thought to consist of red coralline algae, chiefly *Ellisolandia elongata* (J. Ellis et Solander) K. R. Hind et G. W. Saunders, 2013 frequently noted in literature under its former name, *Corallina elongata* J. Ellis et Solander, 1786. Pigments from red algae may impart an orange tint to inner layers of *P. ulyssiponensis* shells. This species is reported [Branch, 1981; Katsanevakis et al., 2008] as a territorial one. After foraging, adults consistently return to their habitats, where deep depressions can be formed due to localized erosion of underlying soft coralline algae. However, research by M. Seabra *et al.* [2019] did not support the hypothesis that *P. ulyssiponensis* larvae preferentially settle on red coralline algae substrates. Laboratory-reared larvae showed similar settlement rates on concrete and stone surfaces. These biological traits suggest that adult *P. ulyssiponensis* are unlikely to migrate from rocky substrates to ship hulls or keels and thus be transported to other areas. Interestingly, settling of larvae on submerged ship surfaces could enable dispersal to new sites: if larvae mature and release fertilized eggs en route, this might facilitate colonization of previously unoccupied water areas.

Regarding the ecology of prosobranchs with short pelagic larval phase, such as *P. ulyssiponensis*, it should be noted as follows: *Patella* species are inhabitants of contour biotopes. These crawling gastropods inhabit hard-substrate communities in the mid-littoral, upper infra-littoral, and partly supralittoral zones along temperate Eastern Atlantic and Mediterranean coasts [Vafidis et al., 2020]. *P. ulyssiponensis* prefers rocky shores with wave exposure levels ranging 1 to 4–5 on the Beaufort scale [Ballantine, 1961], where water turbidity does not impede algal growth. The species is common on open or semi-open coasts, while in sheltered bays, its abundance declines. The primary limiting factor for molluscs is coastal pollution, particularly by toxic surfactants, *inter alia* petroleum derivatives [Black Sea Red Data Book, 1999]. Anthropogenic load is increasing and more and more affecting coastal ecosystems, in particular altering *Patella* habitats and population structures. In the Sochi Port area, *P. ulyssiponensis* settlements were recorded on smooth concrete surfaces (on a buoy and tetrapods) predominantly colonized by green, red, and brown algae, as well as by oysters and mussels. A red coralline alga, typically associated with the primary habitat of this species, was observed rarely – only on a breakwater near the beach of the "Alexandriisky Mayak" apartment complex (sta. 2). Notably, the outer side of the southern pier (sta. 1) hosting a more abundant population benefits from water exchange with the open sea and full-depth water clarity. This station is far from a more polluted semi-enclosed port water area, where transparency is limited to 1–2 m and the seabed consists of silty black sediments emitting a strong hydrogen sulfide odor (see Fig. 1). Improved habitat conditions along the Sochi coast have facilitated *P. ulyssiponensis* distribution in the region.

The occurrence of the population of this species on the Caucasian shelf can be driven by the recovery of the Black Sea ecosystem following a period of eutrophication, with reduced pressure from planktonic predators (the warty comb jelly *M. leidyi*), reduction and shrinkage of the population of the rapa whelk

Rapana venosa (Valenciennes, 1846), and with a shift in climate conditions [Arashkevich et al., 2015; Pereladov, 2013; Sayenko, Marushko, 2018]. Analysis of literature data suggests a current trend toward the recovery of the limpet populations in the southern Black Sea (on the Turkish coast) as well [Aydın et al., 2021; Güngör, Turan, 2019].

Potential pathways of *Patella ulyssiponensis* dispersal in the Black Sea. Currently, *P. caerulea* is recorded in various areas off the Black Sea coast of Turkey [Aydın et al., 2021; Çulha et al., 2007; Güngör, Turan, 2019]. Genetic and morphological analysis and studies of reproductive traits were carried out for this species [Aydın et al., 2021; Güngör, Turan, 2019]. Comparative DNA analysis revealed closely related haplotypes in *P. caerulea* individuals inhabiting the port of Şile area (coast of Turkey) and the Sea of Marmara. According to [Güngör, Turan, 2019], the greatest divergence was observed between the Black Sea population and the Mediterranean one. In the Mediterranean basin, five limpet species are documented: *P. caerulea*, *P. rustica*, *P. ulyssiponensis*, *P. ferruginea*, and *P. depressa*; out of them, only *P. caerulea* is an endemic one [Mauro et al., 2003]. As noted earlier, *P. ulyssiponensis* we studied features significant morphological differences from other Mediterranean *Patella* species. Considering this, we hypothesize substantial genetic divergence between the Black Sea *P. ulyssiponensis* population and the Mediterranean one.

It remains unclear, how did *P. ulyssiponensis* reach the northeastern Caucasian shelf if it has not been recorded along the Black Sea coast of Turkey. Importantly, its absence in published material and in a mollusc collection of the Sochi Geographical Society assembled in the 1960s evidences for the fact that this species disappeared from the Caucasian shelf of the Black Sea in the middle of the XX century. The staff of the Admiral Ushakov Maritime State University carried out summer benthic surveys with scuba diving equipment in the areas of the Sochi port, Khosta breakwaters, and Cape Vidny in 2012–2013 and in Sukhumi port area in 2016–2017 [Selifonova, 2018; Selifonova, Bartsits, 2018; Selifonova et al., 2019]. There were no *P. ulyssiponensis* in fouling communities of piers, breakwaters, rocks, and stones. Since 2012–2014, as already mentioned, researchers from the Sochi Geographical Society registered single *Patella* spp. along the coast from Lazarevskoye to Adler (L. Sonicheva and I. Antonova, oral reports). In 2019–2020, the authors observed a noticeable aggregation of the mollusc not only in Sochi vicinity, but also in Abkhazia, along Pitsunda and Gudauta coasts. Based on shell age analysis, we can conclude as follows: *P. ulyssiponensis* has been spreading along the entire Sochi coast from Adler to Lazarevskoye since approximately 2017–2018. Along the Georgian coast, south of Batumi, *Patella* spp. was recorded in 2017 [Kurakin, 2023].

Let us discuss potential pathways of dispersal (introduction vectors) of this mollusc in the shelf zone of the Caucasian Black Sea coast.

One hypothesis (considering *P. caerulea* finding on the Black Sea coast of Turkey) covers *P. ulyssiponensis* reinvasion from the Mediterranean Sea. Apparently, this transfer of the limpet occurred similarly to the introduction of a gastropod *R. venosa*. According to a widely accepted hypothesis, the rapa whelk was introduced to the Black Sea in the 1940s *via* a ship with a hull carrying its egg cases. An alternative pathway has also been proposed: transport *via* ballast water of ships [Pereladov, 2013]. The same as with *R. venosa*, after *P. ulyssiponensis* introduction to the Black Sea, its morphological and biological characteristics may gain variability under new ecological conditions.

Our study does not dismiss the hypothesis of the limpet transfer *via* fouling of plastic hulls of yachts and boats. An adult specimen could be transported by a passenger vessel if a mollusc was attached

to the submerged ship surface. Sochi hosts the largest passenger port on the Black Sea specializing in cruises to the Black Sea and Mediterranean countries and republics: Abkhazia, Egypt, Georgia, and Turkey (until recently, to Cyprus, Greece, and Israel as well). The Sochi port covers the main seaport in Sochi, eight marine terminals (Imeretinka, Adler, Kurortny, Khosta, Matsesta, Dagomys, Loo, and Lazarevskoye), and the cargo area of the seaport, Sochi Imeretinsky, at the Mzymta River mouth. In literature, just one case of introduction has been described (the only one so far): from the deepwater commercial port of Sines on the Atlantic coast of Portugal [Seabra et al., 2008]. There, a hypothesis was tested in 2005 about different distribution models for *Patella* molluscs on natural rocky substrates outside the port and artificial tidal pools within the port area. Experimentally, the highest density of settled larvae was observed on plastic (on PVC panels). Some researchers report the limpet introduction far beyond marine basins. For example, a lake-type rounded shell of *P. ulyssiponensis*, about 4–5 years old, was washed ashore on a deserted bank of the Volga River in autumn 2022 (the Kuybyshev Reservoir, Ulyanovsk) [Artemyeva, Semenov, 2022]. The authors suggest that the mollusc could have been transported on hulls of river/sea vessels navigating the Volga – Don – Sea of Azov – Black Sea – Mediterranean Sea waterway.

Another potential vector for *P. ulyssiponensis* dispersal is larval transfer *via* coastal currents and ballast water of merchant ships. However, this hypothesis is debatable due to the lecithotrophic larval stage of the limpet which has a short developmental phase. The most plausible scenario is as follows: adult molluscs reached the Caucasian shelf of the Black Sea within enclosed ballast water volumes of ships transporting containers and bulk cargo through the Sochi Imeretinsky area during the construction of the Olympic Park facilities and later (in 2010–2022). Along the Caucasian coast, the Rim Current flows east to west enabling *P. ulyssiponensis* to subsequently spread along the entire Sochi coastline. During summer, catamarans, passenger ships, and recreational boats operate between Sochi and Abkhazia (Sukhumi and Gagra). Accordingly, there is the question: what are potential limits for further limpet expansion in the Black Sea?

Despite existing diagnostic keys, *P. ulyssiponensis* morphological identification remains pretty challenging, as distinguishing traits within the genus are unreliable. This underscores the need for molecular-genetic methods [Sanna et al., 2012]. Those have already confirmed that *P. caerulea* and *P. ulyssiponensis* are separate species *via* comparison of mitochondrial DNA [Sá-Pinto et al., 2005]. The species also differ in chromosome morphology and number: *P. ulyssiponensis* has a haploid set of 8 ones, while *P. caerulea* has 9 [Petraccioli et al., 2010]. Given the pronounced morphological variability of *P. ulyssiponensis* in the Black and Mediterranean seas, only comprehensive genetic analysis can clarify its taxonomic status: is it a species, subspecies, ecomorph, or a case of individual variability.

Conclusions. Based on a literature review of morphological features, biology, and ecology of the Black Sea and Mediterranean *Patella* representatives, as well as analysis of our own material sampled in June 2023, we conclude that an abundant population found in the Sochi port area belongs to the species *Patella ulyssiponensis*.

We assume that the limpet occurrence within the northeastern Caucasian Black Sea shelf is associated with anthropogenic transfer by ships and its subsequent natural dispersal in the region. However, the possibility of a natural recovery of a previously existing local population cannot be ruled out. Available data do not allow a definitive choice to be made between these two hypotheses. A precise determination of *P. ulyssiponensis* occurrence in this area requires comparative genetic studies of *Patella* populations

inhabiting the Black Sea off the Caucasian shores and coast of Turkey. The observed abundant aggregation of the limpet on the Caucasian shelf may be attributed to the recovery of the Black Sea ecosystem following a period of eutrophication, reduced pressure from planktonic and benthic predators (the warty comb jelly *Mnemiopsis leidyi* and the rapa whelk *Rapana venosa*, respectively), and a shift in climate conditions.

Despite the emerging trend of *P. ulyssiponensis* population recovery at one site (along the Caucasian coast in the Sochi port area), long-term ecological effects of its historical decline persist in other Black Sea regions (the Crimea, Ukraine, Bulgaria, and Romania). There, *Patella* representatives remain rare, endangered species. Consequently, due to its conservation status and absence in several coastal zones of the Black Sea, *P. ulyssiponensis* cannot currently be considered a target for commercial harvesting.

Nevertheless, this finding, along with other recent observations, highlights positive shifts in gastropod fauna of the Caucasian Black Sea area.

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БРЮХОНОГИЙ МОЛЛЮСК *PATELLA ULYSSIPONENSIS* GMELIN, 1791 (GASTROPODA: PATELLIDAE) НА КАВКАЗСКОМ ШЕЛЬФЕ ЧЁРНОГО МОРЯ: БИОЛОГИЧЕСКАЯ ИНВАЗИЯ ИЛИ ВОССТАНОВЛЕНИЕ НАТИВНОЙ ПОПУЛЯЦИИ?

Ж. П. Селифонова[1], М. А. Ренева[2], О. П. Полтаруха[3], А. Л. Боран-Кешишьян[1]

[1]Государственный морской университет имени адмирала Ф. Ф. Ушакова, Новороссийск, Российская Федерация

[2]Сочинский национальный парк, Сочи, Российская Федерация

[3]Институт проблем экологии и эволюции имени А. Н. Северцова РАН, Москва, Российская Федерация

E-mail: *selifa@mail.ru*

Весной 2023 г. в районе Сочинского порта обнаружена многочисленная популяция, состоящая из взрослых особей брюхоногого моллюска *Patella ulyssiponensis* Gmelin, 1791. *P. ulyssiponensis*, так называемое морское блюдечко, — контуробионт, ползающий съедобный брюхоногий моллюск; он занесён в Красную книгу Чёрного моря, Крыма и Севастополя и до сих пор отсутствует на шельфе Крыма, Украины, Румынии, Болгарии и Турции. На кавказском шельфе моллюска не находили примерно с середины XX в. В работе приведены данные о распространении, морфологической структуре и плотности поселения моллюсков *P. ulyssiponensis*, собранных в районе Сочинского порта в июне 2023 г. По выраженности радиальных рёбер и их объединению в пучки, положению макушки, морфометрии самой раковины, цвету внутренней поверхности раковины, а также цельности или зубчатости перистомы обнаруженный нами вид был отнесён к *P. ulyssiponensis*, который известен в Чёрном море как *Patella tarentina* Salis Marschlins, 1793, *P. caerulea* var. *tenuistriata* Weinkauff, 1880 и *P. pontica* Milaschewitsch, 1914 (syn.). В более ранних работах по Чёрному морю его объединяли с *P. caerulea* Linnaeus, 1758 — эндемиком Средиземного моря. Плотность *P. ulyssiponensis* в районе Сочинского порта достигала 240–320 экз.·м$^{-2}$

и была выше на станции, расположенной на внешней стороне южного мола, чем в районе пляжей. Изученные нами особи были несколько мельче ранее отмеченных в Чёрном море. Максимальная длина раковины в районе исследования достигала 43,0 мм, ширина — 17,3 мм, высота — 20 мм. Особи из района Сочи имели более высокую раковину, чем особи черноморской популяции и популяции из северной части Эгейского моря, что характерно для обитателей уреза воды. Для первого и второго исследованного местообитания отношение высоты раковины к её длине составляло (0,43 ± 0,05) и (0,45 ± 0,07) соответственно. Реинвазия *P. ulyssiponensis* в северо-восточную часть кавказского шельфа могла быть связана с антропогенным переносом судами и с естественным расселением. Это открытие, наряду с другими аспектами, отмеченными в последние годы в экосистеме Чёрного моря, иллюстрирует позитивные изменения в фауне брюхоногих моллюсков кавказского шельфа.

Ключевые слова: *Patella ulyssiponensis*, распространение, морфометрия, плотность, Сочинский порт